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Abstract

In tropical forests, pioneer species regenerate from seeds dispersed directly into canopy gaps, and from seeds that persisted in soil seed banks before gap formation. However, life-history models suggest that selection for long-term persistence of seeds in soil should be weak, as persistence incurs a fitness cost resulting from prolonged generation time. We use a carbon dating technique to provide the first direct measurements of seed persistence in undisturbed tropical forest seed banks. We show that seeds germinate successfully from surface soil microsites up to 38 years after dispersal. Decades-long persistence may be common in pioneers with relatively large mass, and appears to be unrelated to specific regeneration requirements. In *Croton billbergianus*, a sub-canopy tree that recruits in abundant small gaps, long-term persistence is associated with short-distance ballistic seed dispersal. In *Trema micrantha*, a canopy tree with widespread dispersal, persistence is associated with a requirement for large gaps that form infrequently in old-growth forest.

Introduction

Up to 15 % of tree species in old-growth tropical forests have been classified as pioneers that require high light conditions for successful seedling recruitment (Hubbell et al. 1999, Molino and Sabatier 2001). In most forests these conditions are found in treefall gaps that occur infrequently, at largely unpredictable locations, and that usually only persist for only a few years before canopy closure (Hartshorn 1990, Young and Hubbell 1991, Schnitzer et al. 2000). As a consequence, pioneer life-histories are usually characterized by traits associated with a high colonization ability *i.e.* prolific seed production, high seed dispersability, and disturbance-cued germination from soil seed banks (Whitmore 1983, Swaine and Whitmore 1988).

Despite presumably strong selection for traits that favor the colonization and occupation of gaps, pioneer life-histories are remarkably diverse. On Barro Colorado Island (BCI), Panama, pioneer species vary by over four orders of magnitude in seed mass (Dalling et al. 1998b), and at least two-fold in seedling relative growth rate (Dalling et al. 2004). This trait diversity is maintained by trade-offs that equalize recruitment success (Dalling and Burslem 2005). Seed size variation is maintained by a trade-off between colonization success, selecting for large numbers of small seeds, and emergence and establishment success, selecting for large seed mass (Dalling and Hubbell 2002, Coomes and Grubb 2003). Similarly, variation in seedling relative growth rate can be explained by an inverse relationship between growth and survival rate (Brokaw 1987, Hubbell and Foster 1992, Kitajima 1994, Dalling et al. 1998b).

Trade-offs affecting establishment and growth, however, cannot account for additional interspecific variation observed in seed dispersal ability. Among the pioneers of BCI, median dispersal distances estimated from seed trap data vary from <1 m for some species with dehiscent fruit or ballistic dispersal, to > 60 m for some wind-dispersed tree species (Dalling et al. 2002). Seed burial experiments suggest that significant variation also exists in seed persistence time. While detailed demographic studies of common, small-seeded pioneers have shown that seeds persist for a few years or less (Alvarez-Buylla et al. 1990, Dalling et al. 1998a), some pioneers have seed banks that retain high viability for at least three years even when exposed to predators and decomposer organisms (Hopkins and Graham 1987, Dalling et al. 1997, Murray and Garcia 2002).

The adaptive value of seed persistence is to reduce the impact on plant recruitment of temporal variation in the favorability of habitat conditions (Venable and Brown 1988). In environments where recruitment conditions fluctuate strongly over large spatial scales, seed persistence may provide the only solution to increasing population growth rate, and may be critical to maintaining populations of short-lived or semelparous species. In forests however, interannual variation in the recruitment rates of pioneer species may be as strongly affected by the spatial location of recruitment sites as by the frequency of their occurrence (Dalling et al. 1998b). In these environments therefore, dispersal and seed persistence may have equivalent effects on recruitment success. Nonetheless, selection is expected to favor the evolution of enhanced dispersal as persistence incurs an added fitness cost resulting from delayed reproduction (Venable and Brown 1988). Furthermore, selection on long-term seed persistence should be weak if adult reproductive lifespan exceeds the interval between which favorable recruitment sites become available (Rees 1994, Thompson 2000).

However, selection in favor of dispersal assumes that life-history trait combinations are unconstrained. Increased dispersal ability may carry a cost associated of reduced establishment success, associated with reduced seed mass, or may impose additional constraints on the range of microsites where establishment can successfully occur (Dalling and Hubbell 2002). Here we provide a first step in describing interspecific variation in seed persistence in pioneer trees, using a carbon dating technique to determine the age of viable seeds extracted from natural soil seed banks.

Study Site and Methods

We measured how long seeds of pioneer species remain viable in the soil beneath seasonally moist lowland tropical forest on Barro Colorado Island (BCI), Panama ($9^o10'$N, $79^o51'$W). Rainfall on BCI averages 2600 mm/yr rainfall with a pronounced dry season from January to April (Windsor 1990). Seeds were collected in May 2002 from soil cores taken within old-growth forest in the 50 ha forest dynamics plot in the center of the island (Hubbell and Foster 1983). Only surface soil layers (0-3 cm depth) were sampled to ensure that seeds were collected from burial depths from which emergence can successfully occur (Pearson et al. 2002). Seeds were extracted from the soil by wet sieving, identified to species, and germinated in sand in individual Petri dishes. To increase the probability of encountering 'old' seeds, we used plot data to sample locations where reproductive-sized individuals of focal tree species had occurred over the previous 20 years.

We targeted three relatively large-seeded pioneer species shown to retain high viability over two years in seed burial experiments (Dalling et al. 1997). *Croton billbergianus* (Euphorbiaceae), air-dry seed mass 24 mg, is a ballistically-dispersed sub-canopy tree with a median dispersal distance of 2.2 m (Dalling et al. 2002). *Croton* is among the commonest pioneers on BCI with 367 reproductive-sized individuals recorded in the 1995 census of the 50 ha plot. *Trema micrantha* (Celtidaceae), seed mass 3.9 mg, is a bird dispersed canopy tree with year-around seed production. *Trema* is rare in old-growth forest on BCI; 11 reproductive sized individuals were recorded in the 1995 plot census. *Zanthoxylum ekmannii* (Rutaceae), seed mass 11 mg, is the most abundant of four congeneric dioecious canopy trees on BCI; 108 reproductive individuals were recorded in the 1995 plot census. Median dispersal of *Zanthoxylum* spp was estimated at 0.8 m (Dalling et al. 2002). *Zanthoxylum* fruits are semi-dehiscent follicles that lack an apparent dispersal reward for frugivores. Nonetheless, seeds are reportedly dispersed by primates (Hladik and Hladik 1969).

Samples of seed coat material from 32 seeds that germinated (supplementary table) were cleaned and dated using accelerator mass spectrometry (AMS) at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. AMS yields high precision measurements of $^{14}C/^{13}C$ based on very small amounts of carbon (<100 μg) by providing counts of individual isotope atoms (Donahue et al. 1990, Donahue 1995, Moriuchi et al. 2000). Dates of carbon fixation for the samples were determined by regressing the sample $F^{14}C$ value (Reimer et al. 2005) against a long-term atmospheric record for Northern Hemisphere zone 2 (Hua and Barbetti 2005). Seed dates obtained with this technique are conservative because we assume that carbon fixation occurred during the period of declining $^{14}C/^{13}C$ (post 1963), rather than ascending $^{14}C/^{13}C$ (1953-1963). As an independent check of our ability to accurately date seeds we analyzed fruit and seed wall material from dated herbarium specimens collected and stored on BCI. Specimens used were *Ficus insipida, Hamelia axillaris, Miconia lonchophylla, Ochroma pyramidale, Simarouba amara, Stemmadenia grandiflora*, *Stenospermaton angustifolium* and *Tabebuia rosea* collected between August 1967 and August 1996.

Results and Discussion

AMS carbon dating of herbarium seed material of known age (Fig. 1) shows that predicted ages for field-collected seeds are likely to be accurate within <2 years. With one exception, predicted seed ages and seed collection dates differed by <18 months. Seeds of *Stenospermaton angustifolium*, an epiphytic aroid collected in 1997, however, were predicted to be >4 years older than observed. The age discrepancy for this species probably indicates long-term storage of fixed carbon in rhizomes used for infrequent reproduction.

Application of AMS dating to field-collected seeds indicates that seeds of the three pioneer species tested are capable of persisting in the soil for decades (Fig. 2). Germinable seeds were recovered from surface soil layers after up to 18 yr (*Zanthoxylum*), 31 yr (*Trema*) and 38 yr (*Croton*) in the soil seed bank. These persistence times are remarkable given the rapid decomposition rates of woody material on the soil surface in tropical forests (Chambers et al. 2000).

The costs of AMS prevents dating of sufficient samples to construct survivorship curves for seeds in the seed bank. Nonetheless, the relatively high viability of seeds isolated from the same soil cores from which seeds were dated suggests that long-term persistence is likely to be common for these species (supplementary table). For *Zanthoxylum*, three seeds dated from one soil core gave consistent ages of 15-16 years; 11 % of the 535 seeds recovered from the core were germinable. For *Trema*, five seeds dated from one core gave ages ranging from 20-31 years; 12 % of 100 seeds recovered from the core were germinable. For *Croton*, a sub-canopy tree with very low estimated fecundity (2.6 seeds/cm^2 basal area; Dalling et al. 2002), only ten seeds were recovered from the soil, seven of which were germinable.

The seed ages reported here greatly extend the measured duration of seed persistence times for tropical pioneers. Seed burial experiments have shown that seeds of the majority of pioneer species retain high viability for at least two years (Perez-Nasser and Vázquez-Yanes 1986, Hopkins and Graham 1987, Dalling et al. 1997), but longer-term burial experiments have not been reported. Decadal seed persistence however is consistent with inferred seed persistence times calculated as the ratio of seed bank density to average annual seed rain. Repeated measurements of seed rain and soil seed densities made in a montane forest in Costa Rica yielded a median seed bank to seed rain ratio 8.4 for 23 species (Murray and Garcia 2002). Several species common in the seed bank, including *Trema micrantha*, were not observed in seed rain over three years, while a pioneer shrub *Bocconia frutescens* accumulated a seed bank equivalent to 85 year of seed rain. Estimates of seed persistence based on seed bank to seed rain ratios are sensitive to sampling methods and are unlikely to meet assumptions of spatial homogeneity and temporal equilibrium of seed rain and seed banks (Garwood 1989, Murray and Garcia 2002). Nonetheless, the combination of direct seed dating and inferred seed residence times in the soil strongly suggest that long-term seed persistence is common for tropical pioneer trees and shrubs.

In contrast to field data, population growth models predict that selection for long-term seed persistence should be weak (Murray 1988). This is because seeds that germinate after a long period in the soil contribute less to population growth than those that arrive directly in gaps or germinate soon after dispersal. Long-term seed persistence, however, may arise even if it is not under direct selection. Risk of mortality for seeds is highest shortly after dispersal, when seeds are exposed to predators and pathogens on the soil surface (Estrada and Coates-Estrada 1991, Dalling et al. 1997). Physical and chemical traits that provide sufficient protection for seeds to become incorporated into the soil may incidentally also confer long-term persistence in the soil.

Alternatively, long-term seed persistence may indicate that reproductive models for pioneers require revision. Predictions that long-persistent seeds contribute little to population growth based on population projection models are strongly influenced by parameter estimates for the proportion of seeds that germinate each year (Murray 1985, Murray 1988). Estimates of germination success based on seed sowing experiments in gaps (Murray 1988) are several orders of magnitude greater than observed probabilities of seedling recruitment based on comparisons of seed bank and seedling recruit densities in artificially created gaps (Dalling and Hubbell 2002). Finally, projection models have also assumed that recruitment rates from seed banks are constant over time. Selection for long-term seed persistence may reflect strong inter-annual variation in the timing and frequency of gap formation.

Although species included in this study have similar seed mass they differ in other important respects. *Croton* is slow growing, has short-distance dispersal, and is capable of regenerating in a wide range of gap sizes (Pearson et al. 2003). *Zanthoxylum* appears to have similarly short-distance dispersal, but is among the fastest growing species in the forest (Condit et al. 1993). *Trema* is rare on BCI and is restricted to very large treefall gaps that occur infrequently in old growth forest (Brokaw 1987, Pearson et al. 2003). Thus long-term seed persistence does not appear to restricted to pioneers that share a single combination of life-history traits but instead is likely to be widespread among species in this functional group.

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Supplementary Table: Seeds of the three focal species *Croton bilbergianus*, *Zanthoxylum ekmannii*, and *Trema micrantha*, were collected from sites beneath living or recently dead conspecific adults in the BCI 50 ha forest dynamics plot. Tree tag identifies the individual tree below which trees were collected. Locations of these trees are available from on-line plot census data (www.ctfs.si.edu/datasets/bci). Dates of tree death are known to the five year intervals between censuses of the 50-ha plot (Hubbell and Foster 1983). Seed date gives the predicted date of carbon fixation for each seed. The percent of seeds viable and the total number of seeds recovered is given for each tree location.

Species	Tree Tag	Date of Tree Death	Seed Date	% Seeds viable (n)
Croton	241614	1995-2000	1963.9	100 (3)
Croton	241614	1995-2000	1993.4	-
Croton	241614	1995-2000	1990.4	-
Croton	417588	Alive 2002	2000.1	33 (3)
Croton	135254	1995-2000	1992.7	100 (2)
Croton	135254	1995-2000	1984.2	-
Croton	163343	1995-2000	1999.1	50 (2)
Zanthoxylum	7318	Alive 2002	1999.6	4 (472)
Zanthoxylum	7318	Alive 2002	2000.9	-
Zanthoxylum	7318	Alive 2002	2000.8	-
Zanthoxylum	4240	Alive 2002	1999.6	3 (402)
Zanthoxylum	4240	Alive 2002	2000.1	-
Zanthoxylum	4240	Alive 2002	1995.4	-

Zanthoxylum	4240	Alive 2002	1999.1	-
Zanthoxylum	3846	1995-2000	1987.7	11 (535)
Zanthoxylum	3846	1995-2000	1986.5	-
Zanthoxylum	3846	1995-2000	1987.6	-
Zanthoxylum	3846	1995-2000	1986.1	-
Zanthoxylum	6263	1982-1985	2003.5	22 (54)
Zanthoxylum	6263	1982-1985	2001.6	-
Zanthoxylum	6263	1982-1985	2002.8	-
Zanthoxylum	6263	1982-1985	2001.4	-
Trema	3085	1985-1990	1981.4	12 (100)
Trema	3085	1985-1990	1971.6	-
Trema	3085	1985-1990	1977.4	-
Trema	3085	1985-1990	1980.8	-
Trema	3085	1985-1990	1982.3	-
Trema	4629	1985-1990	1985.3	8 (51)
Trema	4629	1985-1990	1982.1	-
Trema	4629	1985-1990	1976.9	-
Trema	6102	1982-1985	1973.9	66 (9)
Trema	6102	1982-1985	1997.4	-

Figure Legends

Figure 1. Correlation of date of seed production derived from ^{14}C dating with date of seed collection for eight liana and tree species sampled from herbarium sheets. Correlation r=0.99. Error bars are 95 % confidence intervals for the regression of the isotopic ^{14}C ratio determined by mass spectrometry and the atmospheric $F^{14}C$ record for Northern Hemisphere Zone 2 (Hua and Barbetti 2004, Reimer et al. 2004).

Figure 2. Atmospheric record of $F^{14}C$ for Northern Hemisphere Zone 2 (grey points), and predicted dates and their 95 % confidence intervals for the production of individual seeds of a) *Croton bilbergianus*, b) *Trema micrantha* and c) *Zanthoxylum ekmannii* recovered from surface soils in lowland wet tropical forest. Dates for seeds were determined from regressions of seed $F^{14}Cs$ with the atmospheric record.

Fig. 1

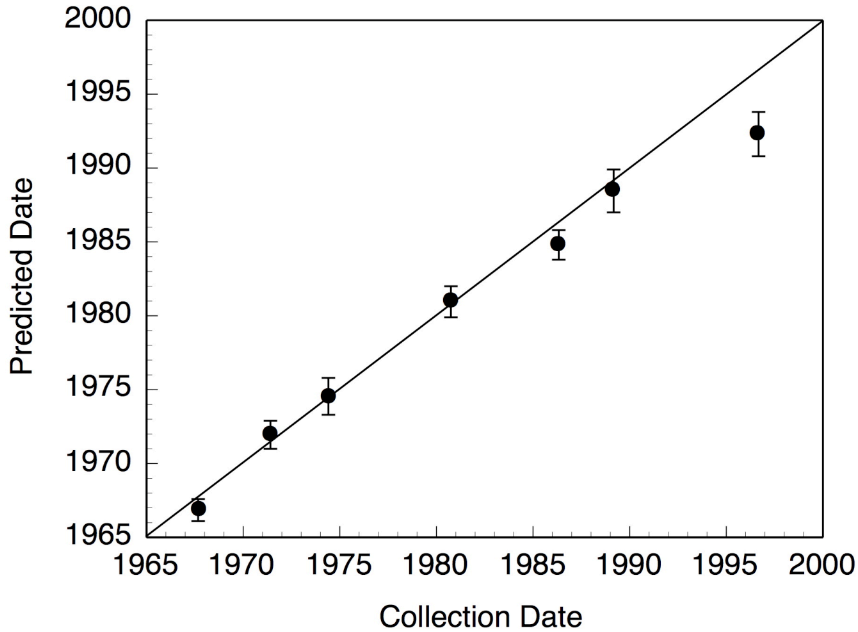
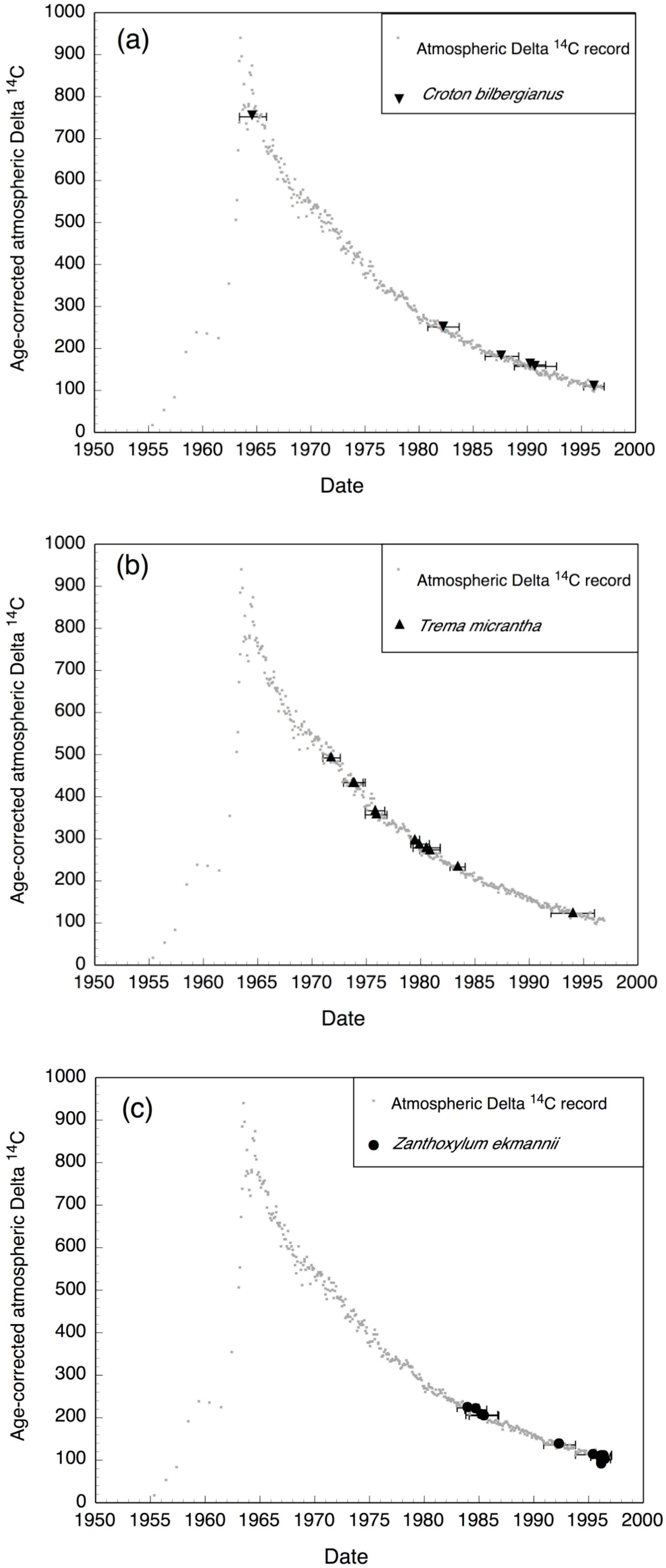

2000
1995
1990
1985
1980
1975
1970
1965
Predicted Date
1965
1970
1975
1980
1985
1990
1995
2000
Collection Date

Figure 2


(a)
Atmospheric Delta ^{14}C record
Croton bilbergianus
Age-corrected atmospheric Delta ^{14}C
Date
(b)
Atmospheric Delta ^{14}C record
Trema micrantha
Age-corrected atmospheric Delta ^{14}C
Date
(c)
Atmospheric Delta ^{14}C record
Zanthoxylum ekmannii
Age-corrected atmospheric Delta ^{14}C
Date